

A retrospective review of the breeding season of the thylacine; Guiler revisited.

Stephen R. Sleightholme¹ and Cameron R. Campbell²

¹ Project Director - International Thylacine Specimen Database (ITSD), 26 Bitham Mill, Westbury, BA13 3DJ, UK. E-mail: DrSleightholme@aol.com

² Curator of the online Thylacine Museum: <http://www.naturalworlds.org/thylacine/>

8707 Eagle Mountain Circle, Fort Worth, TX 76135, USA. E-mail: naturalworlds@yahoo.com

ABSTRACT

The most comprehensive assessment of the breeding season of the thylacine was that undertaken by Eric Guiler of the University of Tasmania in 1961. Guiler based his study on a retrospective analysis of government bounty records. The authors contend that the bounty records contain inherent anomalies that undermine Guiler's findings, and argue that historical newspaper reports, together with museum and zoo records, provide better data to determine the natural boundaries of the breeding season of the thylacine.

Key Words: Thylacine, Tasmanian tiger, *Thylacinus cynocephalus*, breeding season, Eric Guiler, government bounty.

DOI: <http://dx.doi.org/10.7882/AZ.2014.020>

Introduction

Our knowledge of the breeding season of the thylacine (marsupial wolf, or Tasmanian tiger, *Thylacinus cynocephalus*) is largely based on Eric Guiler's (1961) detailed analysis of government bounty records. The authors contend that these records contain inherent anomalies that undermine Guiler's original findings. They argue that historical newspaper reports, together with museum and zoo records, provide better data to determine the natural boundaries of the breeding season of the thylacine.

Bounty Schemes

Following the introduction of commercial sheep farming to Tasmania in the 1820s, the thylacine was expeditiously and somewhat unjustly perceived as a vicious sheep killer, and relentlessly persecuted through a series of government and private bounty schemes. The two principal bounty schemes, i.e., that of the Van Diemen's Land Company (introduced in 1830) and that of the Tasmanian government (introduced in 1888)¹, were instituted as a consequence of persistent lobbying by landowners and farmers to reduce what was perceived to be predation by thylacines on their livestock. In reality, the thylacine was simply a convenient target to blame for all of the stockmen's ills. Its predation on livestock was grossly exaggerated to cover for poorly managed estates, kills by feral dogs, poor pasture, rural depression and rustling. The government bounty of £1 per adult and 10/- for each partly-grown thylacine was terminated in 1909. A total of 2,207 bounties were paid at a cost to the Treasury of

¹ The government bounty was discontinued for all thylacines destroyed from the 1st July 1908, although payments continued to be made into 1909. The bounty legislation was repealed on the 26th April 1909.

£2,132 and 10/- (Paddle, 2000, p.167). The Van Diemen's Land Company bounty scheme was terminated five years later in 1914.

Guiler's 1961 Study

Guiler investigated the surrender dates for sub-adult thylacines submitted for government bounty in the 21-year period between 1888 and 1909. His study comprised 152² thylacines, made up of 52 pups, 45 young and 55 half-grown specimens [Fig. 1].

Guiler's analysis showed that sub-adult thylacines were taken throughout the year. He records a peak submission for pups between May and August, and concludes that an extended breeding season of four months existed, with a degree of out-of-phase breeding. This, Guiler states, "is commensurate with the present concept of dasyure breeding activity". Guiler (1985, p.74) notes that the histograms for pups, young and half-grown show a bimodal distribution, but acknowledges that this may be an artefact due to small sample sizes.

Out-of-Phase Breeding

With reference to Guiler's out-of-phase findings, a number of possible explanations exist.

1. Seasonal Snaring

Snaring was predominantly a seasonal activity, and trappers would often spend several weeks (or even months) in the field before returning home to submit their

² Study comprised 150 sub-adult thylacines submitted for government bounty, plus two additional (unspecified) specimens.

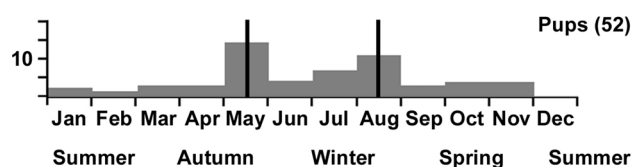


Fig. 1(i). Monthly frequency distribution of the catch of pups.

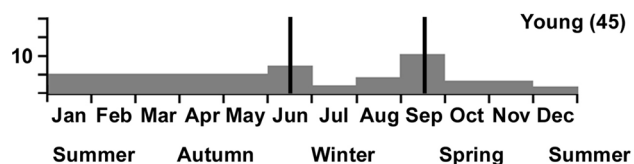


Fig. 1 (ii). Monthly frequency distribution of the catch of young.

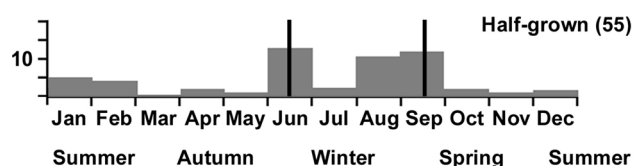


Fig. 1(iii). Monthly frequency distribution of the catch of half-grown thylacines.

Figure 1. Monthly frequency distribution of the catch of pups (i), young (ii) and half-grown thylacines (iii) submitted for government bounty. Peak submissions denoted by black lines. Source: *Journal of Mammology*, Vol. 42 (3), p.397.

skins for bounty. These skins would have been recorded in the bounty records for the month of submission, and not necessarily the month of kill. What Guiler identifies as out-of-phase breeding may be the result of the distortive effect of bulk submissions.

2. Hawking of Skins

The naturalist Michael Sharland, in his book *Tasmanian Wild Life*, notes:

“Over the years many of the animals fell victim to gun and snare, and it was only a man with a deficient sense of business who would be content with the government bounty. With a scalp hanging from the saddle, the hunter rode to homesteads over a wide area and proudly exhibited his catch to each farmer in turn, declaring it had been taken on or adjacent to his farm and thus collecting tribute, the farmer being only too happy to help towards the eradication of any animal that menaced his sheep. Finally, when the odorous relic had reached a condition in which no further hawking for rewards was possible, it was deposited at the nearest police station where the government bounty was handed out. Over the years, therefore, the business of catching the Tiger yielded good returns”.

Geoffrey Watkins Smith, in his book *A Naturalist in Tasmania*, notes:

“A reward of a pound is given for the head by the Government, but the shepherd generally rides round with the head to several sheep-owners in the district, and takes toll from them all before depositing it at the police station. In consequence a large reward must be offered for the carcass of a Tiger, and an offer of £10 during a year for a live Tiger to be delivered in Launceston was unsuccessful. It pays the

shepherd very much better just to hack off its head and take it round on his rides”.

If the hawking of skins by bushmen was common practice (and this does appear to have been the case³), with several weeks or months elapsing between kill and bounty submission, then this too may account for Guiler's out-of-phase findings.

3. Incorrect Grading for Bounty

Guiler (1985, p.74) states: *“The clerks differentiated between pups and half-grown young in about two-thirds of the claims”.* One would assume that most clerks adopted a “small”, “medium” and “large” approach to this type of work, rather than follow any scientific guidelines. Owing to the somewhat arbitrary nature of bounty grading, the incorrect attribution of older offspring as “cubs” or “pups” would undoubtedly have contributed to Guiler's out-of-phase findings. A good example of the misappropriation of the term “cub” can be seen with a female thylacine and her three young sent to the Beaumaris Zoo⁴ in Hobart in 1909 [Fig. 2]. The North Western Advocate and the Emu Bay Times of the 6th July 1909 reported on their capture:

“The auxiliary ketch Gladys, which trades between Stanley and Whale Head, returned on Saturday, and had some rare cargo aboard in the shape of a Tasmanian tiger and three young cubs. They were snared on the V. D. L. Company's property at Woolnorth by the company's overseer (Mr. Thomas Lovell) and Mr. George Wainwright. The animals are being sent to Hobart, and it is said, have realised a nice sum. They were the object of much curiosity at the local port”.

The “young cubs” were in reality the offspring of the 1907 breeding season, and at between half and two-thirds

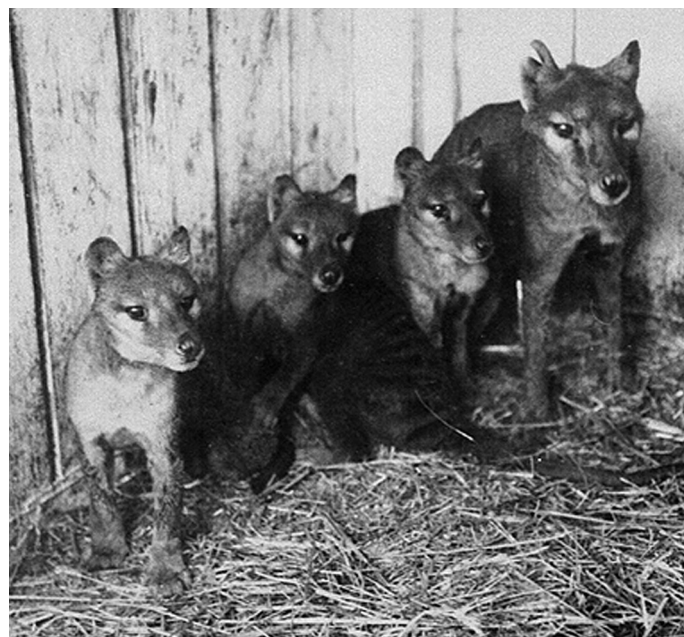


Figure 2. Thylacine mother and young photographed shortly after their arrival at the Beaumaris Zoo in July 1909. Photo, www.naturalworlds.org/thylacine.

³ Pers. comm., Col Bailey, (5th Jan 2013).

⁴ Beaumaris Zoo (at its Sandy Bay location) operated under the ownership of Mary Grant Roberts as a private zoo from 1895-1921.

grown, aged around 21 months when photographed (Paddle, Pers. comm., 28/1/2014). If these thylacines had been graded for bounty as “cubs”, then this would have incorrectly given the impression that they were the progeny of the 1909 breeding season. The following newspaper report is another example of the misappropriation of the term “young”; this time, from the Launceston Examiner of the 18th January 1886:

“The steamer Devon, which arrived on Saturday from North-West coast ports, brought a valuable addition to the Town Park menagerie in the form of a young native tiger or hyena, which was caught at Montagu about two months ago, and recently conveyed to Circular Head by coach. The tiger, which is about three parts grown, had one of its feet injured when caught, but which will it is hoped speedily be cured”.

If the appellation “young” was used when submitting this “three parts grown” tiger for bounty, then this too could be misinterpreted as a much younger individual. In reality, this tiger would have been entirely independent of its mother, and at least 21 months old when caught.

4. Remote Placement for Breeding

By the beginning of the twentieth century, as thylacines became scarce, it would have become increasingly difficult for individuals of breeding age to locate each other to mate. Consequently, the normal breeding pattern of the species may have been disrupted, resulting in some out-of-phase breeding. A well documented example of late mating are the two young pups, a male and female, received by Mary Roberts, the owner of the Beaumaris Zoo, on the 7th May 1912⁵. The pups, still dependent on their mother’s milk, were around three months old when caught, and the likely product of a late November 1911 mating.

5. Disease

Devil Facial Tumour Disease [DFTD] has led to the reproductive season for Tasmanian devils (*Sarcophilus harrisii*) being less well-defined, with births spread throughout the year (Jones *et al.*, 2008, pp. 10023-27 and Owen & Pemberton, 2005, p.66). During the latter part of the 19th and early part of the 20th century, a distemper-like illness decimated thylacine numbers (Paddle, 2012). It is entirely possible, just like the effects of DFTD in devil populations, that disease may have been responsible for some out-of-phase breeding.

Closed Season

As the thylacine became increasingly rare, the Tasmanian Animals and Birds Protection Board granted the species partial protection on the 20th August 1929. This somewhat belated measure appears to have been a reluctant concession to appease the voiced concerns of naturalists. Clive Lord, director of the Tasmanian Museum (1923-1933) and secretary of the Royal Society of Tasmania (1918-1933), was the most vociferous in stating that the species was headed for extinction. A closed season from the 1st to the 31st December came into force on the 6th May 1930. Paddle (2000, p.182)

states: “No records have been preserved in the minutes (of the Tasmanian Animals and Birds Protection Board) that suggest why December was chosen as the minimum one month closed period”. He postulates that as the board members had access to the Lands & Surveys Department’s data from the government bounty scheme, this is why the month of December may have been chosen. Guiler (1985, p.30) states: “The rationale for prohibiting the hunting of thylacines in December was that it was believed to be their breeding season”. As at that time, no study had been undertaken to establish when the thylacine bred, the choice of December as the closed season appears in retrospect to have been somewhat arbitrary.

Bounty Payment Exclusions

Bounty payments were not paid for pouch- dependent young. A story in the Examiner newspaper of the 9th July 1907 confirms this to be the case:

“Two large tigers, male and female, with four young pups in her pouch were caught on the Brookstead estate of Mr Norman White. After conveying them to Fingal, White was rather surprised to find that the authorities would only reward him for the two large ones”.

Thylacine Reproduction

Little is known about the reproductive behaviour of the thylacine. Guiler (1985, p.75) states: “It is assumed from all accounts that thylacines breed once a year and this is in line with the general pattern of reproduction in the Dasyures”. Educated comparisons have been made in the past with the thylacine’s smaller cousins the Spotted-tailed quoll (*Dasyurus maculatus*) and the Tasmanian devil (*Sarcophilus harrisii*), with estimates for the gestation period varying from 21 to 35 days, and for the pouch period from 3 to 4½ months. A shorter pouch period of 3 months, comparable to that of the Spotted-tailed quoll, is now accepted by most authors (Le Souef, Burrell & Troughton, 1926, p.319; Dixon, 1989, p.14; Paddle, 2000, pp.224-233; Sleightholme, Robovsky & Vohralík, 2012, p.237). It is known that at around 16 weeks, thylacine young left the pouch permanently, only returning to suckle (Robison, letter, 26/8/1902, Smithsonian Archives, Box 94), and that they were not fully weaned until around 8 months. The Mercury newspaper of the 12th February 1924 records the arrival of a female thylacine and her three young at the Beaumaris Zoo (Queen’s Domain). The female was caught some 7 months earlier (June 1923) with young in her pouch. With reference to their continued dependence on the mother, the article states: “Although given a supply of chopped up meat, they are not altogether at a stage when they are independent of their maternal diet”. In wild populations, juvenile thylacines remained with their mother for a minimum of 12 months before finally leaving the family unit to lead independent lives. Paddle (2000, p.38) notes: “The first generation of young commenced leaving the family in the months before the next breeding cycle began, and departure was completed (and probably parentally encouraged) before the next generation of young became fully independent of the pouch”.

⁵ Despite best efforts, both pups died on the 10th May 1912.

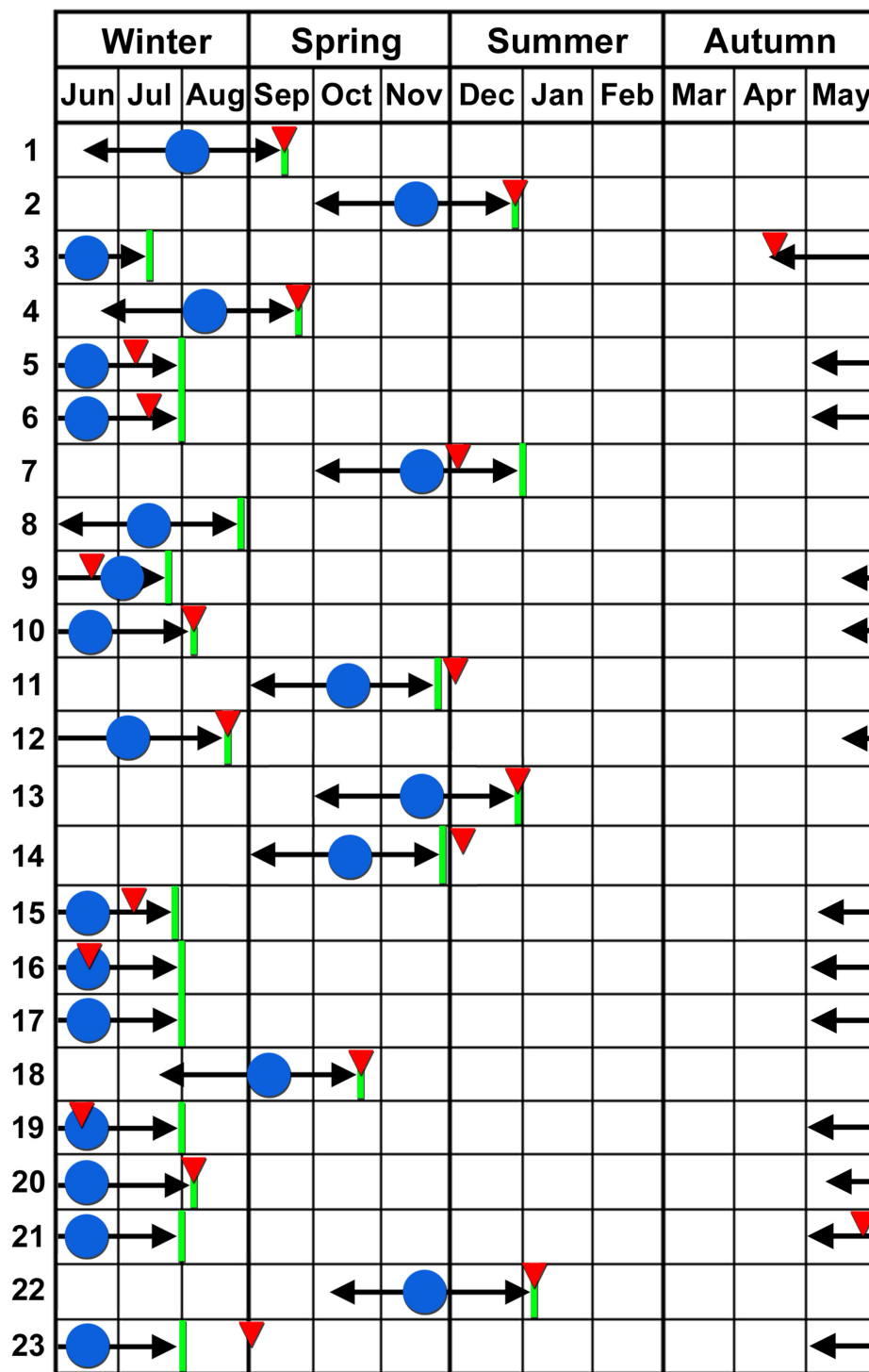


Table I. Table showing months when female thylacines (n=23) were captured or killed with pouch-dependent young, together with the known or estimated pouch period and its termination.

Key: Closed arrows = known or estimated period of pouch occupancy, Green line = known or estimated end of pouch occupancy, Blue circle = known or estimated mid-point (6 weeks) of permanent pouch occupancy, Inverted triangle = date of observation (excludes entry 8, as this is a retrospective observation made in February 1924 regarding the arrival at the Beaumaris Zoo of a family group caught earlier that year).

Source Data: [1] Mercury, 19th Sep 1898, Female & 4 pouch young, [2] Star, 29th Dec 1862, Female & 4 pouch young, [3] ITSD 4th Revision (2011), 3rd Sep. 1902, Washington Zoo pups (Smithsonian Records) – Prof. Heinz Moeller retrospectively estimated the birth date for the National Zoo's litter as being 15th April 1902 ± 1 week (letter 19/05/2007), [4] Mercury, 26th Sep 1884, Female & 4 pouch young, [5] Examiner, 9th Jul 1907, Female & 4 pouch young, [6] Mercury, 16th Jul 1886, Female & 4 pouch young, [7] Hobart Town Gazette, 2nd Dec 1896, Female & 4 pouch young, [8] Mercury, 12th Feb 1924, Female & 3 pouch young, [9] ITSD 4th Revision (2011), Museum Victoria, 23rd Jun 1909, Female & 4 pouch young, [10] Examiner, 4th Aug 1893, Female & 3 pouch young, [11] Hobart Town Gazette, 2nd Dec 1826, Female & 4 pouch young, [12] Launceston Examiner, 20th Aug 1889, Female & 3 pouch young, [13] Melbourne Zoo captive births, Jan 1900, Paddle, 2000, p. 229, [14] Australian Museum Archive C: 40.66 / 7th Dec 1866, George Masters' pouch young specimen [AMS P762], [15] Mercury, 5th Jul 1884, Female & 4 pouch young, [16] The Courier, 16th Jun 1858, Female & 3 pouch young, [17] Burnie Advocate, 15th Feb 1986, Female & 2 pouch young, [18] Mercury, 20th Oct 1884, Female & 4 pouch young, [19] Mercury, 13th Jun 1905, Female & 4 pouch young, [20] Mercury, 5th Aug 1924 p. 7, Female & 2 pouch young, [21] Alfred Cleland - St. Helens Police Station on 29th May 1893, Female & 2 pouch young, Paddle Pers. comm., 26th March 2013, [22] Reid interview with Paddle, 27th February 1992, Female with two pouch young arrived at the Beaumaris Zoo (Domain) on 10th January 1928, [23] Edward Dearing interview, 1st January 1974, Transcript of notes in Jeremy Griffith Collection (CH, QVMA), Female with 3 pups.

The Historical Record

As the government bounty excluded pouch-dependent young, and the somewhat amorphous appellations “young” or “pup” were essentially terms applied to young at heel, we need to look to other sources for evidence as to when breeding historically took place. One reliable source is the Tasmanian press. Thylacine captures or kills, many heroically embellished, were regularly featured in local newspaper reports. Other sources include zoo and museum records. A comprehensive survey of historical Tasmanian newspapers (pre-1936) was undertaken, together with a review of museum and zoo records, to locate articles or registry entries that cite female thylacines with offspring. As the descriptions “pup”, “young” and “cub” have been shown to be somewhat elastic terms, only those reports and registry entries that were reliably dated, and specified pouch occupancy, were collated (Table 1).

The historical accounts rarely make reference to the stage of development, and one has to assume that pouch young would have been beyond the earliest stages of their ontogeny to warrant specific recognition. We have therefore made the assumption that all observations (unless otherwise stated) refer to young in their second or third month, with a degree of error of ± 1 month. The majority of historical accounts are of 19th-century origin, which reduces the possibility for distortions in the breeding cycle as a result of scarce encounter and disease.

With one notable exception, these records show that females with pouch young were caught or killed from the end of May (late autumn) to early December (summer). The noted exception being a female with three pouch young purchased by the City Park Zoo in Launceston shortly before 10th April 1902 (Paddle, Pers. comm., 26th March 2013).

With a gestation period estimated at around 28 days, mating would normally occur from April to September [Fig. 3 (A)]. As the thylacine’s prey species are most abundant during spring and summer, this cycle is commensurate with

maximising food supplies for the young when they become independent of the family unit the following year. No females with pouch young could be located in the historical record between January (summer) and the early part of April (autumn). The entries in Table 1 for the month of December all refer to full-grown pouch young, which would infer that the breeding season was drawing to a close.

In Michael Sharland’s regular “Peregrine” column, published in the Mercury newspaper of the 29 October 1938, he makes the following comments regarding the pouch period for marsupial young:

“Kangaroos and wallabies have young in the pouch through the Winter; the Tasmanian devil carries its baby in its warm marsupial pouch till the Spring, and the “tiger” does the same, although the last named is just as likely to deposit its young ones in some sheltered nook while it is seeking food, and tend to them there until they are large enough to fend on their own account”.

Sharland’s remark with respect to the thylacine is consistent with the historical findings. Paddle (2000, p.56) states:

“Adolescent thylacine movement out of the family and migration across the countryside would commence in late autumn / early winter”.

This observation is consistent with the historical accounts.

Discussion

The bounty records upon which Guiler based his breeding season parameters are essentially dates for the payment of bounty; nothing more or less. Submission peaks in the bounty records would, by virtue of the distortions caused through bulk submission of skins, hawking, and incorrect grading, not necessarily reflect the true breeding pattern of the thylacine. This consideration potentially undermines Guiler’s conclusions, and justifies a revision of his findings. Guiler (1985, p.76) states:

“Mating probably takes place in December or thereabouts since the young would then be born in January and reach the pup or half-grown stage by June - September and start an independent life by early summer”.

There are two major conflicts in Guiler’s statement.

Conflict 1

Such rapid growth in thylacine young after leaving the pouch is contrary to current thinking. Development of the newly independent young into adulthood appears to have been prolonged. Evidence to support this is noted by Paddle (2000, p.226) in his argument for captive breeding occurring at the Melbourne Zoo. The preserved skin of a female thylacine born at the zoo in 1899 (Museum Victoria specimen NMV C5600), reliably aged to around 22 months at its death, was some way from achieving average adult size [Fig. 4]. Paddle notes with reference to the measurements of the specimen skin:

“This is a long way short of currently accepted developmental estimates that suggest that, by the end of just their first twelve months thylacines were probably around three-quarters grown”.

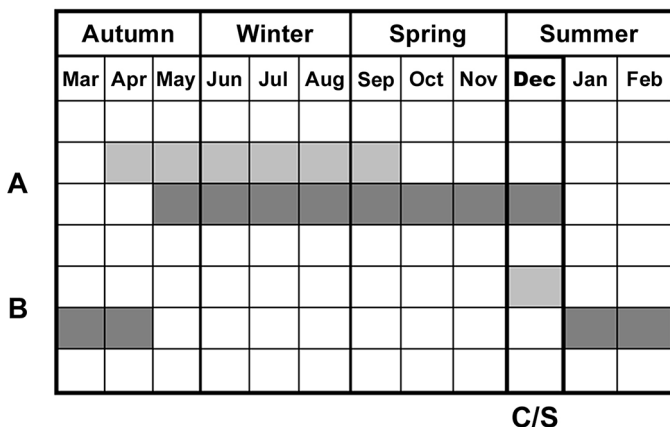


Figure 3. A comparison of the thylacine mating season (light grey) and period when females carry pouch young (dark grey), as determined by (A) Sleightholme & Campbell, (B) Guiler (1961)⁶. C/S = Closed Season.

⁶ Guiler (1985, p.74) estimates the pouch period at 130 - 140 days (4 - 4½ months). A shorter pouch period of 3 months is now accepted by most authors.



Figure 4. Specimen skin NMV C5600. Photo, Museum Victoria. Source: ITSD, 4th Revision, 2011.

It appears, therefore, that at around twelve months, and not six as Guiler suggests, thylacines are near to half their adult size (half-grown). Individuals less than 1 year of age would have accordingly been classed as either young or pups. Sub-adults of various ages would consequently be presented for bounty throughout the year, thus obscuring the natural boundaries to the breeding season.

Conflict 2

No females with pouch young were recorded within the historical newspaper records for the months of January to April, the period when Guiler states that pouch young should be present. The authors have only been able to locate one non-press reference to support a mid-autumnal start to the breeding season, this being a female thylacine with three pouch young purchased by the Launceston City Park Zoo in April 1902, and subsequently sold to the National Zoo in Washington, D.C. later that year⁷.

⁷ The Launceston family group of a mother and three young arrived at the National Zoo in Washington, D.C. on the 3rd September 1902.

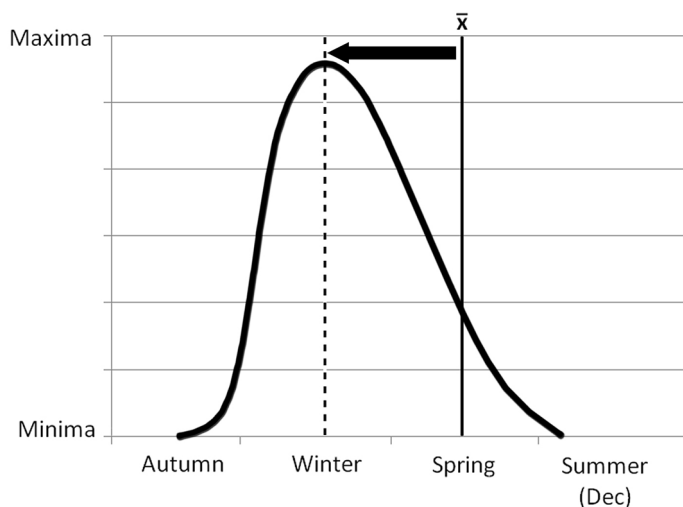


Figure 5. Curve illustrating the breeding cycle of the thylacine with a seasonal maximum (dotted line) positively skewed in favour of the winter months.

As the species became increasingly rare at the turn of the 20th- century, it is highly probable that scarcity of encounter was the underlying factor responsible for this early start to the breeding season. With mating occurring in December as Guiler suggests, the maxima in the breeding cycle would occur between January (summer) and April (autumn) [Fig. 3 (B)]. Dixon (1989, p.14) echoes Guiler's account. This assumption is inconsistent with historical findings. Paddle (2000, p.56) cites females with pouch young from mid-autumn (April) through to December. Therefore, Paddle's findings are in broad agreement with the historical record.

Historical Record Synopsis

Retrospective observational studies involving rare or endangered species are inevitably characterised by small sample sizes. This is especially so when dealing with historical rather than present-day data sources. Although

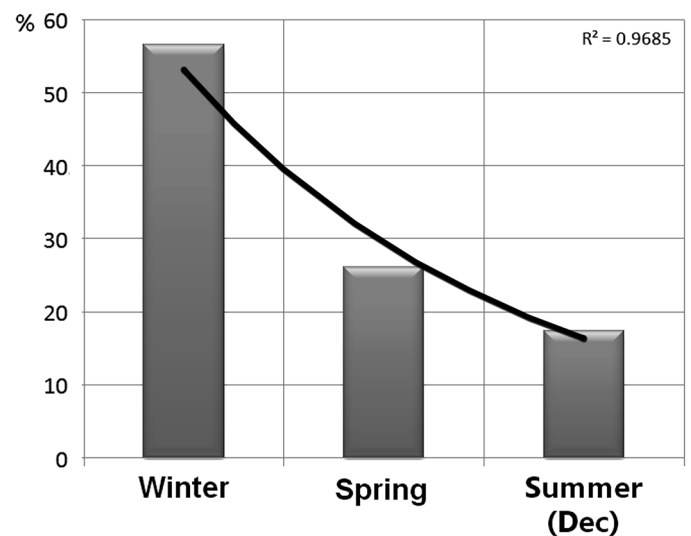


Figure 6. From the historical record, the percentage of females with young at the end of the period of permanent pouch occupancy for winter, spring and early summer (Dec) [TL = Expon].

a greater sampling error is associated with these samples, they are often sufficient to determine statistical significance. Small data sets can also be of value in generating realistic hypotheses and testable models (Bissonette, 1999). The quality of the data is an important factor in smaller studies (Ersbøll & Ersbøll, 2003). The information provided by the historical newspaper, museum, and zoo records, citing specific dates and pouch occupancy, fulfils this criterion in being both reliable and accurate.

It is all too easy to generalise small sample results beyond the appropriate boundaries (Bissonette, 1999), but the absence of evidence for breeding occurring outside the confines of a late autumn to spring interval challenges Guiler's findings, and warrants an alternative hypothesis based on the historical record. This demonstrates that the breeding cycle of the thylacine was unimodal, with a seasonal maximum in the winter months (June, July and August) with the bulk of values situated to the left of the mean [Fig. 5]. 57% of thylacines with pouch-dependent young were found within this period, compared to 26% for spring (Sept/Oct/Nov), and 17% for early summer (December) [Fig. 6]. Bimodality as observed by Guiler does not appear to be evident, and out-of-phase breeding appears to have been a rare event.

Conclusion

A closer examination of Guiler's findings tells us little of when breeding actually occurred, as the boundaries between pups, young and half-grown are obscured by inconsistencies in the bounty data. The authors contend that Guiler's original four-month estimate for the breeding season of the thylacine was based on bounty data masked by bulk submission of skins, hawking, and the questionable classification of young. We provide an alternative hypothesis based on the historical record of females caught or killed with pouch-dependent young. We fully acknowledge the limitations of this small sample size, but contend that historical newspaper, museum, and zoo accounts provide a more accurate survey of when breeding actually occurred. These records show that the thylacine's mating season extended from April through to September, with little evidence to support significant out-of-phase breeding. Females with pouch-dependent young could normally be found from May through to December, and with young at varying stages of their development throughout the year. As such, a closed season at the termination of the breeding cycle would have conferred little, if any, protection to the species.

Acknowledgements

The authors would like to thank Bob Paddle for his valued input on thylacines with pouch young procured for zoological gardens and for his thoughts on the prolonged development of thylacine young. They would also like to thank Col Bailey for his comments on the hunting practices of Tasmanian bushmen. The authors would like to express their thanks to Mike Archer of the Evolution

of Earth & Life Systems Research Group, School of Biological, Earth & Environmental Sciences at the University of New South Wales, and Andrew Kitchener, Principal Curator of Vertebrates at the National Museum of Scotland, for their review and comments on the manuscript.

References

- Bissonette, J. A. 1999. Small sample size problems in wildlife ecology: a contingent analytical approach. *Wildlife Biology*, 5:2, pp. 65-71.
- Dixon, J. M. 1989. Thylacinidae, pp. 1-20 in: D. W. Walton and B. J. Richardson (eds.), *Fauna of Australia, Mammalia*, Vol. 1B. Canberra: Australian Govt. Printing Service.
- Ersbøll, A. K. & Ersbøll, B. K. 2003. Epidemiological Studies Based on Small Sample Sizes – A Statistician's Point of View. *Acta Vet. Scand. Suppl.* 98, pp. 127-40.
- Guiler, E. R. 1961. The breeding season of the thylacine. *J. Mamm.* 42 (3), pp. 396-97.
- Guiler, E. R. 1985. *Thylacine: The Tragedy of the Tasmanian Tiger*, OUP.
- Jones M. E., Cockburn A., Hamede R., Hawkins C., Hesterman H., Lachish S., Mann D., McCallum H. & Pemberton D. 2008. Life-history change in disease-ravaged Tasmanian devil populations, *PNAS*, 105 (29), pp. 10023-27.
- Le Souef, A. S., Burrell, H. & Troughton, E. le G. 1926. *The Wild Animals of Australasia: embracing the mammals of New Guinea and the nearer Pacific islands: with a chapter on the bats of Australia and New Guinea*. Sydney: G. G. Harrap, p. 319.
- Owen, D. & Pemberton, D. 2005. *Tasmanian Devil: A unique and threatened animal*. Crows Nest, New South Wales, Allen & Unwin, p. 66.
- Paddle, R. N. 2000. *The Last Tasmanian Tiger; The History and Extinction of the Thylacine*, Cambridge University Press.
- Paddle, R. N. 2012. The thylacine's last straw: epidemic disease in a recent mammalian extinction, *Australian Zoologist*, 36 (1), pp. 75-92.
- Sharland, M. 1962. *Tasmanian Wild Life*, Melbourne University Press, p. 5.
- Sleightholme, S. R. & Ayliffe, N. P. 2011. *International Thylacine Specimen Database, 4th Revision, Electronic Resource - DVD Rom*, Zoological Society London.
- Sleightholme S. R., Robovský J. & Vohralík V. 2012. Description of four newly discovered thylacine pouch young and a comparison with Boardman (1945), *Australian Zoologist*, 36 (2), pp. 232-238.
- Smith, G.W. 1909. *A Naturalist in Tasmania*, Clarendon Press, Oxford, pp. 96-97.